

A REVISION OF THE GENUS ACRADENIA (RUTACEAE) *

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THE AUSTRALIAN GENUS *Acradenia* Kippist is known to occur naturally from the Macpherson Range on the Queensland–New South Wales border, south, discontinuously, to western Tasmania (see MAP 1).

Since its discovery in the mid-1800's, *Acradenia* has almost universally been considered to consist of a single species, *A. frankliniae*, endemic to Tasmania. Only Mueller (1868 and 1868a) suggested otherwise when he observed that the eastern Australian *Bosistoa sapindiformis* (correctly known as *B. pentacocca*, the type species of *Bosistoa*) might be better placed in *Acradenia*, and proposed for it the name *Acradenia bosistoi*. This idea was not accepted by subsequent authors, and, indeed, Mueller had erred. *Bosistoa pentacocca* has multi-ovulate carpels and buds with scales, and is clearly not congeneric with *Acradenia frankliniae*.

I have found, however, that *Bosistoa euodiiiformis*, described by Mueller from northeastern New South Wales in 1875, is congeneric with *Acradenia frankliniae*, and that the sole species of the genus *Luerssenidendron* Domin, *L. monostylis*, is conspecific with *Bosistoa euodiiiformis*. The purpose of this paper is to revise *Acradenia* in view of this new information.

Acradenia is distinguishable from all known genera of Rutaceae in the Australasian–Malesian region by the following combination of characters: leaves opposite, flowers 5-merous, stamens twice the number of the petals, carpels each with two ovules, and fruits follicular. The prominent carpellary glands of *Acradenia* are also distinctive, although similar structures are found in at least two other genera of Australasian–Malesian Rutaceae, namely, *Flindersia* and *Pentaceras*.

As might be expected, considering its relict-like geographic distribution, *Acradenia* does not have any particularly close generic affinities. *Bosistoa*, *Medicosma*, and *Zieria* are perhaps the most similar of the Australasian–Malesian Rutaceae, but they are obviously not close relatives of *Acradenia*. The need for caution in accepting the traditional classification of the Rutaceae is evident here, as it was in my study of *Acronychia* (Hartley, 1974). Although *Acradenia* was placed along with about 20 other genera in the tribe Boronieae by both Bentham (1863) and Engler (1896 and 1931), it is equally, if not more closely, related to several genera placed by those authors in the tribe Zanthoxyleae. It is worth noting that a Chilean genus, *Pitavia*, has carpellary glands that are remarkably similar to those of *Acradenia*, but it differs in having indehiscent fruits and 4-merous flowers.

This study is based on herbarium specimens. The contributing herbaria (with abbreviations, where available, from Holmgren & Keuken's *Index Herbariorum*, ed. 6. Part I. Regnum Vegetabile. p. 92. 1974) are as fol-

* This is the ninth in a series of papers on the Rutaceae of Malesia and Australasia.



MAP 1. Distribution of the genus *Acradenia*: *A. euodiiiformis* (F. Muell.) Hartley (dots) and *A. frankliniae* Kippist (triangles).

lows: Arnold Arboretum of Harvard University, Cambridge (A); State Herbarium of South Australia, Adelaide (AD); British Museum (Natural History), London (BM); Queensland Herbarium, Brisbane (BRI); Botanical Survey of India, Calcutta (CAL); C.S.I.R.O. Herbarium Australiense, Canberra (CANB); Botany Division, Department of Scientific and Industrial Research, Christchurch (CHR); New South Wales Forestry Commission, Coffs Harbour (COFFS HARBOUR); Gray Herbarium of Harvard University, Cambridge (GH); The University of Tasmania, Hobart (HO); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); National Herbarium of Victoria, Melbourne (MEL); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); Herbarium of the University of California, Berkeley (UC); National Museum of Natural History (Department of Botany), Smithsonian Institution, Washington, D. C. (US); and Naturhistorisches Museum, Wien (W). I wish to thank the directors and curators of these herbaria for making specimens in their care available to me.

Acradenia Kippist, Proc. Linn. Soc. London 2: 201. 1853; Trans. Linn. Soc. London 21: 208. 1854. TYPE SPECIES: *Acradenia frankliniae* Kippist.

Luerssenidendron Domin, Bibliot. Bot. 22(89): 289. 1927. TYPE SPECIES: *Luerssenidendron monostylis* Domin.

Shrubs or trees; indumentum of simple trichomes; buds naked. Leaves opposite, digitately trifoliolate, pinnately veined, with pellucid, punctate or pustular oil glands. Inflorescences paniculate, subcorymbose. Flowers bisexual; sepals 5 (rarely 6), basally connate, valvate, persistent in fruit; petals 5 (rarely 6), distinct, imbricate, plane (neither hoodlike nor apically hooked), deciduous in fruit; stamens twice the number of the petals, the antesealous about as long as the petals, the antepetalous slightly shorter, filaments straight, sublinear, tapering to a subulate apex, anthers 2-celled, dehiscent by longitudinal slits, versatile, broadly elliptic, bluntly mucronulate; disc intrastaminal, pulvinate to columnar, usually angled between the filaments; gynoecium 5- (rarely 4-) carpellate, carpels basally connate and joined adaxially at about the middle by a single style, otherwise contiguous, each with a prominent upper abaxial gland, 1-locular, placentation upper axile, the placenta toward the apex of and protruding into the locule, ovules collateral, 2 per locule, style straight, twisted, about twice the length of the carpels, stigma scarcely differentiated. Fruit of 1-5 basally connate, 1-seeded follicles, undeveloped carpels, if any, persistent; follicles erect, obovate-truncate, transversely ribbed, dehiscent along the apical and adaxial edges; epicarp (the two outer layers of the pericarp — the exocarp and the mesocarp) dry at maturity, subwoody; endocarp cartilaginous, discharged (probably forcibly) with the seed. Seed narrowly to broadly and obliquely pyriform; testa brown, smooth, polished, pergamentaceous; endosperm fleshy, scant; embryo straight, obo-

vate, cotyledons plano-convex, emarginate at the point of attachment of the hypocotyl, hypocotyl terminal, subglobose.

The two species of *Acradenia*, while unquestionably distinct, are nevertheless very closely related, their only significant differences being vegetative. In view of their geographically discontinuous, eastern Australian-Tasmanian distribution (MAP 1) and their ecological preference for temperate rain forests, it seems likely that they have descended from a more widely distributed Tertiary population.

During the Tertiary there was land connection between Tasmania and the Australian mainland, and, up through the Eocene, climatic conditions were such that temperate rain forests were more widespread than in subsequent times. In the middle and late Tertiary there was a general climatic shift, from mild and humid conditions to a drier and cooler climate, by the onset of the Pleistocene. This brought about contraction and fragmentation of the Australian temperate rain forest areas, and may have produced geographic isolation that led to speciation in *Acradenia*.

Speciation may, however, have occurred at a later date. During the Pleistocene in Australia, there were at least two periods when there was broad land connection between Tasmania and the mainland, and an unknown number (at least three or four) of alternating wet and dry periods. These climatic oscillations almost certainly caused expansions and contractions of temperate rain forest areas in southeastern Australia. If one of these expansions was great enough, and also coincided with a suitable Tasmanian-mainland connection, then there may have existed a continuous population of *Acradenia* between Tasmania and southeastern Queensland. Speciation might then have occurred after this continuous population became discontinuous. (In the above discussion, data regarding events of the Tertiary and Pleistocene were obtained largely from Australian biogeographical studies which include summaries of the geological literature, for example, Burbidge (1960), Keast (1961), and Rawlinson (1974).)

An alternative explanation for the origin of these species is that the geographic isolation that led to speciation was the result of long-distance dispersal. This is not a likely possibility, however, because the wingless seeds of *Acradenia* clearly have no adaptation for dissemination of more than a few hundred meters. Another point against long-distance dispersal as a possible explanation is given below.

Further evidence concerning the origin of the two species of *Acradenia* comes from the study of two other pairs of vicarious species of Australian plants whose ranges and ecological preferences are closely homologous with those of *Acradenia*. These are the two Australian species of evergreen *Nothofagus*, *N. cunninghamii* (Hook. f.) Oersted and *N. moorei* (F. Muell.) Krasser,¹ and the two species of the genus *Anopterus* (Escalloniaceae), *A. glandulosus* Labill. and *A. macleayanus* F. Muell. The distribu-

¹The only other species of *Nothofagus* in Australia, *N. gunnii* (Hook. f.) Oersted, an endemic of alpine regions of Tasmania, is deciduous and has a different type of pollen from that found in the two evergreen species (cf. van Steenis, 1971).

tional data given below for the species of *Anopterus* and *Nothofagus* were obtained from Bauer (1957), Curtis (1956 and 1967), Francis (1970), Fraser & Vickery (1938), R. D. Hoogland (personal communication), Moore (1893), and Willis (1973).

Nothofagus cunninghamii occurs in both Tasmania, where it is characteristic of temperate rain forests, and south central Victoria, where it usually lives in wet sclerophyll forests. *Nothofagus moorei* is known only from mountain rain forests from the Barrington Tops Plateau, New South Wales (about 40 miles north of the Hunter River, which is the southern boundary of the range of *Acradenia euodiiiformis*), north to the Macpherson Range. Thus, with the exception of the Victorian population of the former, *Nothofagus cunninghamii* and *N. moorei* have about the same geographic distributions, respectively, as *Acradenia frankliniae* and *A. euodiiiformis*.

Anopterus glandulosus is endemic to Tasmania, where it occurs in wet sclerophyll forests and temperate rain forests. *Anopterus macleayanus* is restricted in its distribution to rain forest habitats from Port Macquarie, New South Wales, north to the Macpherson Range. Thus, the distributions of these two species closely match those of *Acradenia frankliniae* and *A. euodiiiformis*.

It is evident, as van Steenis (1971) has pointed out, that *Nothofagus* is not adapted for long-distance dispersal. Also, the fossil record provides ample evidence that *N. cunninghamii* and *N. moorei* are relicts. *Anopterus*, on the other hand, is obviously well adapted for wind dissemination, having light-weight, winged seeds. In spite of this, I do not think that long-distance dispersal provides the correct explanation for the origin of its two geographically disjunct species. The distance between their two areas (about 800 miles) is not particularly great by long-distance dispersal standards, and it seems that if such dispersal and establishment happened once, it would have happened several times, thus preventing speciation by the repeated introduction of the original genotype.

The geographical and ecological similarities between these species of *Nothofagus*, *Anopterus*, and *Acradenia* may be interpreted as evidence that their two groups of vicarious species (*Nothofagus moorei*, *Anopterus macleayanus*, and *Acradenia euodiiiformis* in the north; *Nothofagus cunninghamii*, *Anopterus glandulosus*, and *Acradenia frankliniae* in the south) are relict assemblages, and that the three genera have been together for a very long period of time during which geographic isolation and speciation occurred. *Nothofagus* pollen of the *menziesii* type, found in *N. cunninghamii* and *N. moorei*, is known from several Tertiary deposits (Eocene to Pliocene) ranging from northeastern New South Wales to southern Victoria (cf. Cookson, 1946), so it is likely that the *Nothofagus-Anopterus-Acradenia* assemblage dates back to that period.

The possibility that the two modern species of *Acradenia* are each part of a relict assemblage of similarly vicarious species considerably strengthens the case against long-distance dispersal.

I have found no evidence that one of the species of *Acradenia* is more

primitive than the other, so they are arranged alphabetically in the following taxonomic section.

KEY TO THE SPECIES

1. Rather small to large tree; branchlets smooth; petiole 1–7.5 cm. long; leaflets 4–23 cm. long; inflorescences 6–21 cm. long. 1. *A. euodiiformis*.
1. Shrub or small tree; branchlets pustular-glandular; petiole 0.3–0.8 cm. long; leaflets 2–6 cm. long; inflorescences 2–5 cm. long. 2. *A. frankliniae*.

1. *Acradenia euodiiformis* (F. Muell.) Hartley, comb. nov.

FIGURE 1.

Bosistoa euodiiformis F. Muell. Frag. Phytogr. Austral. 9: 174. 1875 (as "*euodiformis*"). TYPE: *Wilcox*, New South Wales, upper Clarence River.

Luerssenidendron monostylis Domin, Bibliot. Bot. 22(89): 289. t. 29. 1927.

TYPE: *Moore*, New South Wales, head of Hastings River.

Rather small to large tree to about 30 m.; branchlets pubescent when very young, becoming glabrous, neither glandular nor glaucous. Leaves pustular-glandular and often sparsely puberulent when very young, becoming punctate and entirely glabrous; petiole 1–7.5 cm. long; leaflets



FIGURE 1. *Acradenia euodiiformis* (F. Muell.) Hartley. Flowering branchlet (drawn from *Jones 13*), $\times \frac{1}{3}$.

narrowly elliptic to oblanceolate, 4–23 cm. long, 1.2–6.5 cm. wide, base cuneate to attenuate, midrib evident but usually not prominent, main veins visible but usually faint, 8–12 on either side of the midrib, margin entire or, less often, crenate toward the apex, apex obtuse to acute or occasionally acuminate. Inflorescences from the axils of the upper leaves, several- to many-flowered, 6–21 cm. long; peduncle, upper axis, and branches sparsely puberulent to glabrate; pedicels sparsely puberulent to glabrate, slender, 4–12 mm. long. Flowers 6–6.5 mm. long; sepals green, 5, sparsely pubescent abaxially, ciliate on the margin, triangular, 1–1.5 mm. long; petals white to cream, 5, tomentose abaxially, sparsely pubescent adaxially, elliptic to narrowly obovate, 5.5–6 mm. long; stamens with glabrous filaments, anthers 1.5 mm. long; disc glabrous, 0.5–0.8 mm. high; carpels 5, tomentose except for the glabrous, upper abaxial gland, 1.5–2 mm. high; style glabrous. Follicles tomentose, 6–8 mm. high; endocarp glabrous. Seed about 5 mm. long.

ILLUSTRATION. Domin, K. *loc. cit.* (as *Luerssenidendron monostylis*).

DISTRIBUTION. Macpherson Range, southeastern Queensland, south to the Hunter River, New South Wales; rain forests to 1200 meters. See MAP 1.

Queensland. MORETON DISTRICT. Macpherson Range: 0.4 km. beyond turn-off to Picnic Rock, West Canungra Creek, *Smith 11290* (BRI); road to Moran's Falls, near Lamington National Park, *Smith 14187* (BRI); Moran's Creek Paddock, Lamington Plateau, *Whaite 3032* (NSW); upper Coomera River, Balmamboolah Falls, *Perry 507* (CANB); Roberts Plateau, *O'Reilly*, September, 1929 (BRI), *White*, January, 1919 (BRI); Lamington National Park, near Mt. Hobwee, *White 6172* (A, BRI, NY, UC), *6172A* (A, BRI); Lamington National Park, O'Reilly's Guest House, *Smith*, December, 1963 (BRI), *Smith & Webb 3641* (BRI), *Webb 5008* (CANB); Lamington National Park, *Moore 54* (BRI), *Tryon & White*, March, 1920 (A, NSW, P), *White & Tryon*, March, 1920 (BRI); Springbrook, *Rudder 4018* (BM, K), September 6, 1929 (BRI), September, 1930 (A). New South Wales. Whian Whian State Forest, *Constable*, January 15, 1953 (L, NSW 22341, US), *Hayes*, January, 1953 (COFFS HARBOUR), *Jones 13* (BRI), *351* (BRI), *951* (CANB), October, 1966 (BRI), *Moriarty 703* (BRI, CANB), *1689* (CANB), *1690* (CANB), *Webb & Tracey*, 1953–1958 (BRI, CANB), July, 1956 (BRI); Bangalow, *Baeuerlen*, December, 1896 (NSW 128875); Tintenbar, *Baeuerlen 590* (NSW), September, 1893 (NSW 128877); upper Clarence River, *Wilcox*, November, 1875 (MEL, holotype of *Bosistoa euodiiformis* F. Muell.); Clarence River, *Beckler* (MEL); Chapmans Plains, *Hayes & McGillivray*, October 27, 1966 (COFFS HARBOUR); Dorrigo State Forest, *Davis*, October 15, 1955 (AD), *White 7562* (A, BRI, NY); Dorrigo, *Boorman*, March, 1909 (NSW 128879), September, 1909 (NSW 128880), *Fraser*, January 23, 1934 (NSW 128881), *Vickery*, April 15, 1953 (NSW 128882); Mobong Creek, *Hayes*, October 29, 1953 (COFFS HARBOUR); Bruxner Park, *Anonymous*, October 16, 1952 (COFFS HARBOUR), *Schodde & Hayes 3532* (A, CANB); about 25 miles W of Urunga, *Hayes & McGillivray 2508* (NSW); upper Taylors Arm, *Hayes*, August 15, 1952 (COFFS HARBOUR); McLeay River, *Anonymous*, 1895 (MEL), *McDonald*, 1894 (MEL); head of Hastings River, *Moore* (K, holotype of *Luerssenidendron monostylis* Domin; GH, isotype); 5 miles SE of Yarrowitch, *Johnson*, October 19, 1953 (NSW 128883); upper Myall

River, *Rupp*, September 29, 1924 (NSW 128888); Doyles River Road about 48 miles W of Wauchope, *Garden*, October 6, 1951 (NSW); Mt. Boss State Forest, South Branch of Wilson River 15 miles NW of Wauchope, *Constable*, October 31, 1956 (NSW 128884); Port Macquarie, *Anonymous*, July, 1891 (NSW 128885); Doyles River State Forest, 30 miles NW of Taree, *Constable 6317* (BRI, NSW); Dingo State Forest, 15 miles W of Wingham, *Schodde 5117* (CANB); Bo Bo Creek, *Jones*, June, 1946 (COFFS HARBOUR); Comboyne, *Chisholm*, November, 1923 (NSW 128887); Ellenborough Falls, *Maiden & Boorman*, October, 1902 (NSW 135709, w); upper Allyn River, *Floyd*, October 31, 1972 (COFFS HARBOUR); Booral, *Rudder*, October 30, 1892 (NSW 128889); Hunter River, *Rudder 3* (MEL).

There is no doubt that *Luerssenidendron monostylis* and *Bosistoa euodiiiformis* are conspecific. It is surprising that Domin did not recognize this, because he saw material of the latter species. (However, the type of *L. monostylis* was in flower, while material of *B. euodiiiformis* lacked flowers.) Instead, he tried to relate *L. monostylis* to *Pagetia monostylis* F. M. Bailey, stating that on the basis of Bailey's description and illustration (Queensl. Dept. Agr. Bot. Bull. No. 13. 7. 1895; Queensl. Fl. 1: 203. 1899; Comprehensive Cat. Queensl. Pl. 80. t. 61. 1909), the two appeared to be identical. They are not, and Domin may have suspected this since he designated a different type for *L. monostylis* and gave no indication that he intended to make a new combination.

2. *Acradenia frankliniae* Kippist, Proc. Linn. Soc. London 2: 201. 1853; Trans. Linn. Soc. London 21: 208. t. 22. 1854. TYPE: *Milligan 1038*, April, 1842, western Tasmania, Franklin River.

FIGURE 2.

Erect shrub or small tree to about 7 m.; branchlets sparsely to densely puberulent, pustular-glandular, usually becoming glaucous. Leaves pustular-glandular; petiole densely puberulent to glabrous, 0.3–0.8 cm. long; leaflets with scattered appressed hairs above and below or glabrous throughout, narrowly elliptic to oblanceolate, 2–6 cm. long, 0.5–2 cm. wide, base cuneate, midrib prominent, lateral veins not visible, margin entire toward the base, crenate toward the apex, apex rounded to obtuse. Inflorescences terminal or terminal and from the axils of the upper leaves, few- to several-flowered, 2–5 cm. long; peduncle covered with rather coarse, appressed hairs, upper axis and branches sparsely puberulent to glabrous; pedicels sparsely puberulent to glabrous, slender, 5–10 mm. long. Flowers 5–7 mm. long; sepals green, 5 (in occasional flowers, 6), sparsely pubescent abaxially, ciliate on the margin, ovate to broadly elliptic, 1–1.5 mm. long; petals white, 5 (in occasional flowers, 6), tomentose abaxially and adaxially in bud, becoming sparsely pubescent, broadly elliptic, 4.5–6 mm. long; stamens with glabrous filaments, anthers 1–1.2 mm. long; disc glabrous, about 0.5 mm. high; carpels 5 (in occasional flowers, 4), tomentose except for the glabrous, upper abaxial gland, about 1 mm. high; style glabrous. Follicles tomentose, 6–8 mm. high; endocarp sparsely hairy on the inner surface. Seed about 5 mm. long.



FIGURE 2. *Acradenia frankliniae* Kippist. Flowering branchlet (drawn from Milligan 727, November 6, 1846), $\times \frac{2}{3}$.

ILLUSTRATIONS. Curtis's Bot. Mag. 153: *t.* 9187. 1927. Kippist, R. *loc. cit.* Rodway, L. Tasmanian Fl. opp. pg. 22. 1903. Stones, M. and W. M. Curtis, The endemic flora of Tasmania. Part 5. *t.* 167. 1975.

DISTRIBUTION. Pieman River south to the Gordon and Franklin Rivers in the vicinity of Macquarie Harbour, western Tasmania; stream margins in temperate rain forests at lower elevations. See MAP 1.

Tasmania. Pieman River at Corinna, *Jackson 258* (HO), *Olsen*, January 14, 1941 (HO); Pieman River, *Gilbert*, February, 1947 (HO), *Simson 1735* (MEL); Macquarie Harbour at Brisbanes Bay, *Milligan 727*, August 17, 1846 (MEL), 727, November 6, 1846 (GH, NY), 727, November 15, 1846 (MEL), 727, March 9, 1847 (K); Macquarie Harbour, *Milligan 727*, October 6, 1846 (K, W), 727 (GH, K, MEL, NY, P), *without number or date* (A, CAL); road to Macquarie Harbour, *Milligan 1038*, 1842 (HO); King River, *Somerville*, April 22, 1947 (HO); Gordon River, banks of Big Creek 8 miles from the mouth, *Milligan 727*, October 12, 1846 (K); Gordon River, *Anonymous*, November 24–27, 1937 (HO), *Olsen*, December 13, 1946 (HO), *Somerville*, January, 1949 (HO); Franklin River, *Atkinson*, November, 1932 (HO), *Milligan 1038*, April, 1842 (K, holotype), 1038, February 8, 1845 (K); without definite locality, *Anonymous*, February 3, 1867 (MEL). CULTIVATED. New Zealand. New Plymouth, *Sykes 918/62* (CHR).

EXCLUDED NAME

Acradenia bosistoi F. Muell. Pap. Proc. Roy. Soc. Tasmania 8: 8. 1868, and Frag. Phytogr. Austral. 6: 167. 1868, *nomen illegit.* (*in obs.* and based on *Euodia pentacocca* F. Muell.) = *Bosistoa pentacocca* (F. Muell.) Baill.

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HERBARIUM AUSTRALIENSE

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